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This report covers our activities since September 15, 1986. The main accomplishments have been: 1) a comprehensive study of the effects of chromatic content, blur and contrast of targets on vernier acuity and on stereo acuity; 2) the use of a new method of measuring chromatic discrimination under conditions of constant adaptation; 3) continuation of the study of the chromatic properties of single cells in the monkey cortex; and 4) experiments on the significance of color in the perception of motion.

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PROGRESS REPORT
September 15, 1986 to March 14, 1989

SUMMARY

This report covers our activities since September 15, 1986. The main accomplishments have been: 1) A comprehensive study of the effects of chromatic content, blur and contrast of targets on vernier acuity and on stereo acuity; 2) The use of a new method of measuring chromatic discrimination under conditions of constant adaptation; 3) Continuation of the study of the chromatic properties of single cells in the monkey cortex; and 4) Experiments on the significance of color in the perception of motion.

BACKGROUND

The main goal of our work is to understand the role of higher-order mechanisms in color vision. By higher-order mechanisms is meant those processes beyond the receptor level and beyond the conventionally-understood opponent color mechanisms.

Krauskopf, Williams and Heeley (1982), using an habituation procedure, found evidence for three sets of independent mechanisms selectively responsive to stimuli varying along three cardinal directions in color space. Two of these directions are chromatic and the third is a luminance axis. Following this, Derrington, Krauskopf and Lennie (1984) found two classes of parvocellular neurons in the monkey LGN, each maximally sensitive to modulation in time of uniform fields in one of the cardinal chromatic directions.

In subsequent research, Krauskopf, Williams, Mandler and Brown (1986) found psychophysical evidence for mechanisms selectively responsive to stimuli in other than the cardinal directions. Krauskopf, Zaidi and Mandler (1986) made measurements of simultaneous color contrast using a nulling technique and concluded that this phenomenon could not be explained in terms of the properties of receptor or second stage mechanisms. In electrophysiological experiments, Lennie, Sclar and Krauskopf (1987) have discovered neurons in primary visual cortex (V1) of monkey that respond best to stimuli modulated along non-cardinal directions which may be part of a system of higher-order mechanisms.

GENERAL METHODS

The results of Krauskopf, Williams and Heeley (1982) and Derrington, Krauskopf and Lennie (1984) have led us to use the color space depicted in Fig. 1 to describe the stimuli in our experiments. The central point of this space is an equal-energy white. There are two chromatic axes which lie within the isoluminant plane through the origin. Along one of these axes the input to the short wavelength (B) cones is constant while the long wavelength (R) and middle wavelength (G) cone inputs covary to keep luminance constant. This is called the Constant B axis. The other chromatic axis is one along which only the B cone input varies and is called the Constant R&G axis. The third axis is one along which the inputs to all three classes of cones vary proportionally and is called the Luminance axis.

These cardinal axes are similar but clearly different from the classical "opponent processes" in that while variation along the Constant B axis produces stimuli that appear reddish or greenish, variation along the Constant R&G axis produces stimuli that appear yellowish-green and purplish, not unique yellow and unique blue. Stimulus variation along the luminance axis results in changes in brightness with no change in hue.

For convenience of exposition the words red, green, yellow and blue and the initials R, G, Y and B will be used to describe stimuli varying along the isoluminant cardinal axes. Changes along the Luminance axis will be called increments and decrements or white and black.

All the stimuli in the experiments discussed here were generated on a television display driven under computer control using an Adage frame buffer system. This system allows linear control of the intensity of the three television primaries to nearly 10-bit accuracy. The spatial resolution is approximately one pixel per minute of visual angle.

PSYCHOPHYSICAL EXPERIMENTS

Offset Thresholds:

There has been a good deal of speculation recently on the properties of separate systems for the processing of stimuli defined by luminance variation ("luminance mechanisms") and stimuli defined by isoluminant chromatic variation ("chromatic mechanisms"). In particular it has been held that chromatic mechanisms are not as efficient as luminance mechanisms in processing spatial information (Livingston and Hubel, 1984; Morgan and Aiba, 1985). In order to test this notion a comprehensive set of experiments has been performed to examine the effects on vernier (offset) acuity of the chromatic content, blur and contrast of the test targets.

We have measured offset thresholds for targets with gaussian spatial profiles defined either by luminance or by chromatic contrast with respect to a neutral background. The tests were defined by excursions in each of the six cardinal directions. Thus they appeared "reddish", "yellowish", "greenish", "bluish" if isoluminant with the background or as luminance increments or decrements with respect to the equal-energy white background. The contrast of the targets was varied from the lowest level at which judgements could be made to the maximum contrast that could be achieved in that chromatic direction. The effect of blur was evaluated by varying the standard deviation of the gaussian profile.

In order to decide whether chromatic mechanisms are less efficient at spatial discrimination than luminance mechanisms, it is necessary to equate the effective contrast of isoluminant and luminous stimuli. We did this by scaling the contrast of the targets used in the offset threshold experiments by their contrast thresholds. Thus, we plotted offset thresholds as a function of log contrast relative to contrast threshold for stimuli in each of six color directions (Fig. 2 and 3). In Fig. 2 the results are for a narrow target ($\sigma = 2.6$ minutes of arc), while in Fig. 3 the results are for a very blurred target ($\sigma = 21.2$). The least-squares regressions for all the stimuli in each panel are drawn through the data points.

If chromatic mechanisms were less efficient in processing spatial information than are luminance mechanisms, we would expect the offset thresholds for chromatic targets to plot above those for luminance targets. The overall impression from most of the results of this experiment is that offset thresholds vary markedly as a function of contrast and as a function of blur; but they are approximately the same for luminance and isoluminant stimuli of equal contrast and blur. The most marked violation of this rule is illustrated in Fig. 2. Here the offset thresholds for the luminance targets (both increments and decrements) plot below the regression line and those for isoluminant targets tend to plot above the regression line. The other observer in this experiment showed similar results, but the advantage of narrow luminance targets over chromatic targets was less pronounced for her.

What might explain the advantage of narrow luminance targets in this experiment? The Fourier transform of a spatial gaussian is a gaussian centered at zero cycles per degree. The narrower the spatial gaussian the broader the transform. Thus the narrow targets have significant energy at high frequencies and at DC. The modulation sensitivity curves for luminance targets are band pass while those for isoluminant targets are low pass. Therefore the DC component of the chromatic stimuli, which provides no information about offset, contributes to their detectability but not that of the luminance targets. This factor may result in the small superiority of the narrow luminance targets. To test this explanation, we measured offset thresholds for targets whose horizontal profiles were odd-symmetric gabor functions. A gabor function is the product of a sine function and a gaussian. Its transform is a gaussian symmetrically disposed about the frequency of the sine term. An odd-symmetric gabor has no DC component. We expected the slight superiority of the luminance targets to disappear for gabor targets and it did. Offset thresholds for such targets are plotted as a function of log contrast relative to detection threshold in Fig. 4 for luminance targets and for isoluminant targets. The frequency of the sine component of the gabors varies over a 16-fold range, from 0.25 cycles per degree to 4.00 cycles per degree. No advantage for either luminance or chromatic stimuli was found.

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These results provide a comprehensive set of data on the effects of contrast and blur on offset thresholds. The results are in accord with a theory that offset judgements depend on the evaluation of the mean local sign of the distribution of the effective photons in the top and bottom elements of the stimulus. The slopes of the lines in Fig. 4 are very close to -0.5, that is, the offset thresholds vary inversely with the square root of the contrast. This is the expectation from the law of large numbers, for the reliability of the mean of a sample distribution as an estimate of the population mean improves as the square root of the number of samples (photons). Similarly, the effect of blur agrees with the expectation of statistical theory. The unreliability of the mean as an estimate of the population mean increases linearly with the standard deviation of the sample.

We have also used the same methods to see whether stereoscopic depth thresholds are higher for chromatic targets than for luminance targets when they are equally above detection threshold. The results are incomplete at this time but it is fairly clear that red and green (Constant B) targets are as good for stereoscopic acuity as luminance targets. The data suggest that Constant R&G targets may, indeed, be inferior for stereo.

Color Discrimination under Constant Adaptation:

One of the central problems of color vision is how discrimination varies over color space. MacAdam (1942), in a classical experiment, had observers make color matches to a variety of stimuli using a method of adjustment. He used the standard deviation of the matches as a measure of discriminability. By using matching stimuli that varied in different directions about the standard stimuli he was able to construct equal-discriminability ellipses about points throughout the C.I.E. chromaticity chart. In MacAdam's procedure, the observer's adaptation level was determined by the standard stimulus and thus was different for each ellipse.

We were interested, for both theoretical and practical reasons, in measuring chromatic discrimination under conditions of constant adaptation. The observer's state of adaptation was controlled by viewing a uniform square 10 degrees on a side displayed on a television monitor. The stimulus pattern, shown in Fig. 5, consisted of three test (T) discs of one color and a fourth comparison (C) disc differed in some direction in color space from them (Fig. 6). In any session the difference between the comparison and the test stimulus was either along the cardinal direction (C2 and C4) or orthogonal to it (C1 and C3). The observer's task was to identify the location of the C disc which varied randomly from trial-to-trial. The threshold difference between the T and C stimuli was estimated by using a 3 to 1 staircase procedure.

Sample results are shown in Figs. 7 and 8 for adaptation to an equal energy white. In one case the difference between the T and C stimuli were in the same direction from the adaptation point (Fig. 7). For example, when the test pulse was reddish and the comparison stimulus was either redder or greener than the test, thresholds increased linearly with the amplitude of the test. On the other hand, when the difference between the test and comparison stimuli is in a direction orthogonal to the direction of the test vector, the thresholds are independent of the magnitude of the test vector (Fig. 8).

When the adaptation point is a saturated red rather than a neutral white (Fig. 9), the thresholds for detecting changes in the reddish and greenish directions are a minimum at the adaptation point. This agrees with the classical finding of Craik (1938) that luminance thresholds tend to be a minimum when the test luminance is equal to the adaptation level.

These data present a very orderly picture and one that differs considerably from that revealed the MacAdam class of experiments. This is not surprising since in the one case the adaptive state varies while in the other adaptation is kept constant. The conditions of the MacAdam experiment may well have allowed the adaptation state to be neither constant at one point in color space nor fixed at the point in color space at which the discriminations are made. We have measured discrimination in different directions about the point at which the observer is adapted and obtained very orderly results. When the adaptation point moves along the Constant B axis discrimination thresholds remain constant. When the adaptation point moves along the Constant R&G axis discrimination thresholds along that axis vary in proportion to the excitation of the short-wavelength sensitive cones. The adaptation effects along the two cardinal axes are independent.

The MacAdam experiment and our experiment relate to different practical situations. The MacAdam experiment is relevant to the case in which one is making a side-by-side comparison of two samples. In

this case one is adapted to the level of the stimuli being compared. But in many situations the observer is scanning a variegated scene and is thus neutrally adapted. Here the data obtained in our experiment would be more relevant than MacAdam's in predicting peoples ability to discriminate under neutral-adaptation conditions, as when color samples are separated.

Significance of color in the perception of motion

We have obtained quite surprising results concerning the role played in the perception of motion by the mechanisms selectively responsive to modulation along the cardinal directions of color space. Drifting gratings modulated along different cardinal directions appear to slip with respect to one another. When the directions of the modulations are rotated by 45 degrees, the gratings cohere.

We think these results have important implications with regard to the mechanisms for processing motion. They make doubtful the notion that there are separate pathways for the processing of color and motion. The idea that only the magno-cellular pathways is significant in the processing of motion is challenged by these results. We conclude that information about movement is conveyed within mechanisms maximally responsive along the cardinal directions to a high level in the processing chain.

NEUROPHYSIOLOGY

Derrington, Krauskopf, and Lennie (1984) showed that the responses of LGN cells to uniform fields and to moving gratings modulated in color confirmed the theory that the cells responses are proportional to the sum of the responses of the cones that drove the cells. The responses of these cells are proportional to the cosine of the angle between the direction of chromatic modulation and the direction of modulation to which the cell responds best. Lennie, Sclar and Krauskopf (1985) have been applying the same methods to single neurons in V1, the primary visual cortex, of the monkey.

With few exceptions, most of the cells in V1 conform to the linear model, or, for complex cells, an extension of it that assumes linear summation of cone signals by mechanisms that generate rectified responses. The distribution of the directions of best responses of cells in V1 differs considerably from that for the LGN. The direction of preferred modulation of many cells in V1 was close to the luminance axis, while this is not true for LGN cells.

Krauskopf, Williams, Mandler, and Brown (1986) reported that observers could discriminate isoluminant targets perfectly at threshold when the stimuli were separated by 90 degrees in color space. This was true for stimulus pairs on either the cardinal axes or 45 degrees from the axes. They argued that this implied the existence of units more selective than is consistent with the linear summation model. Of the 272 V1 cells studied, six showed chromatic selectivity that was more tightly tuned than predicted by the linear model. Cells of this sort might serve as the substrate for these discriminations.

It is remarkable that many of the properties that might be expected of visual cells have not yet been found in these physiological experiments. For example, we have been particularly alert for signs of habituation following strongly effective stimuli since psychophysical habituation provided important evidence of the existence of mechanisms tuned to the cardinal directions. Similarly, it might be expected that cells which were precisely tuned to respond either to stimuli varying in luminance or to isoluminant stimuli should be found, but with the exception of the few cells mentioned above this is not the case. Also, our results disagree with those of Livingston and Hubel (1984) in that we found that neurons that were located in regions rich in cytochrome oxidase were indistinguishable in their chromatic preferences from those in the interstices.

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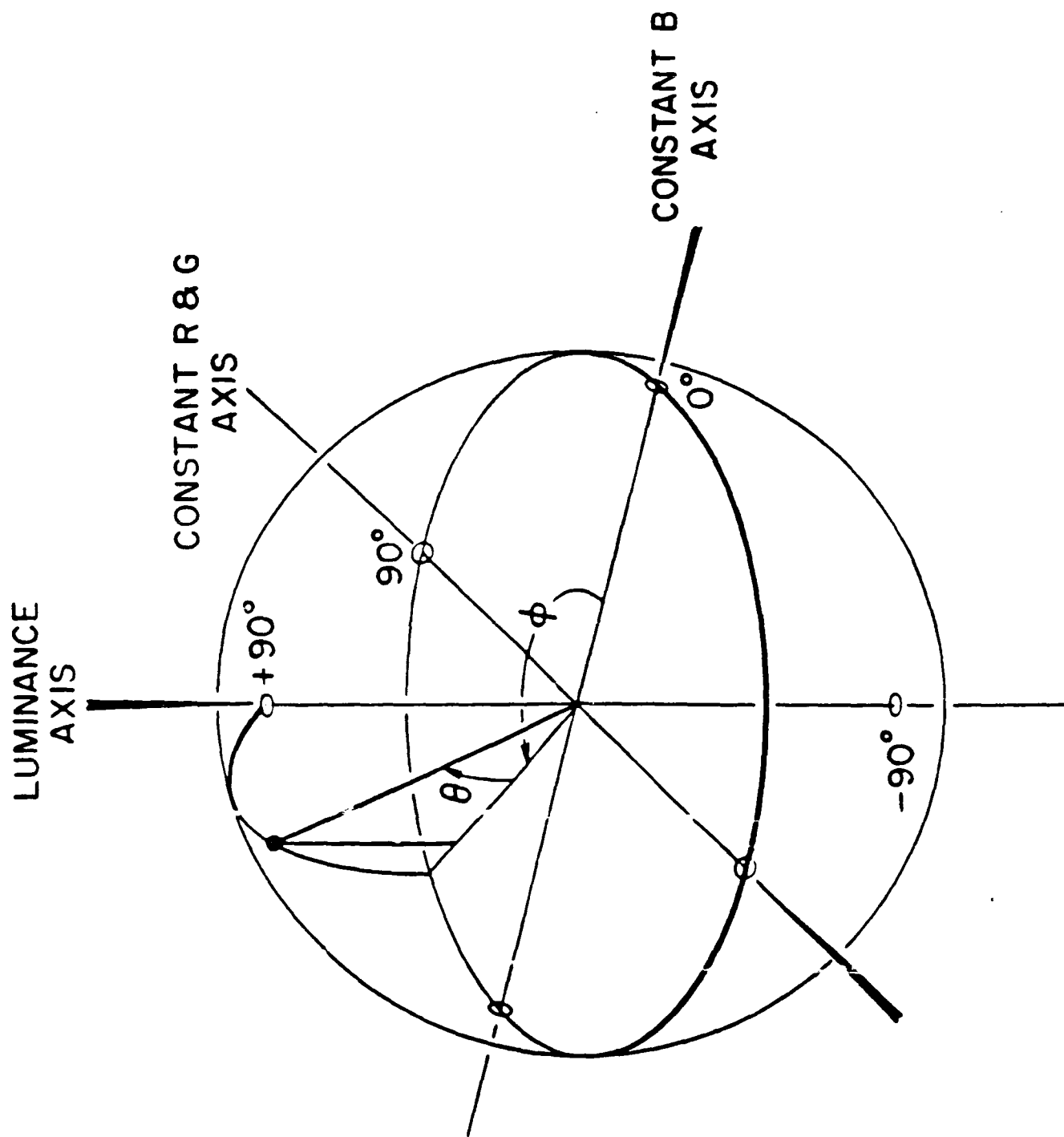


FIGURE 1

OFFSET THRESHOLDS

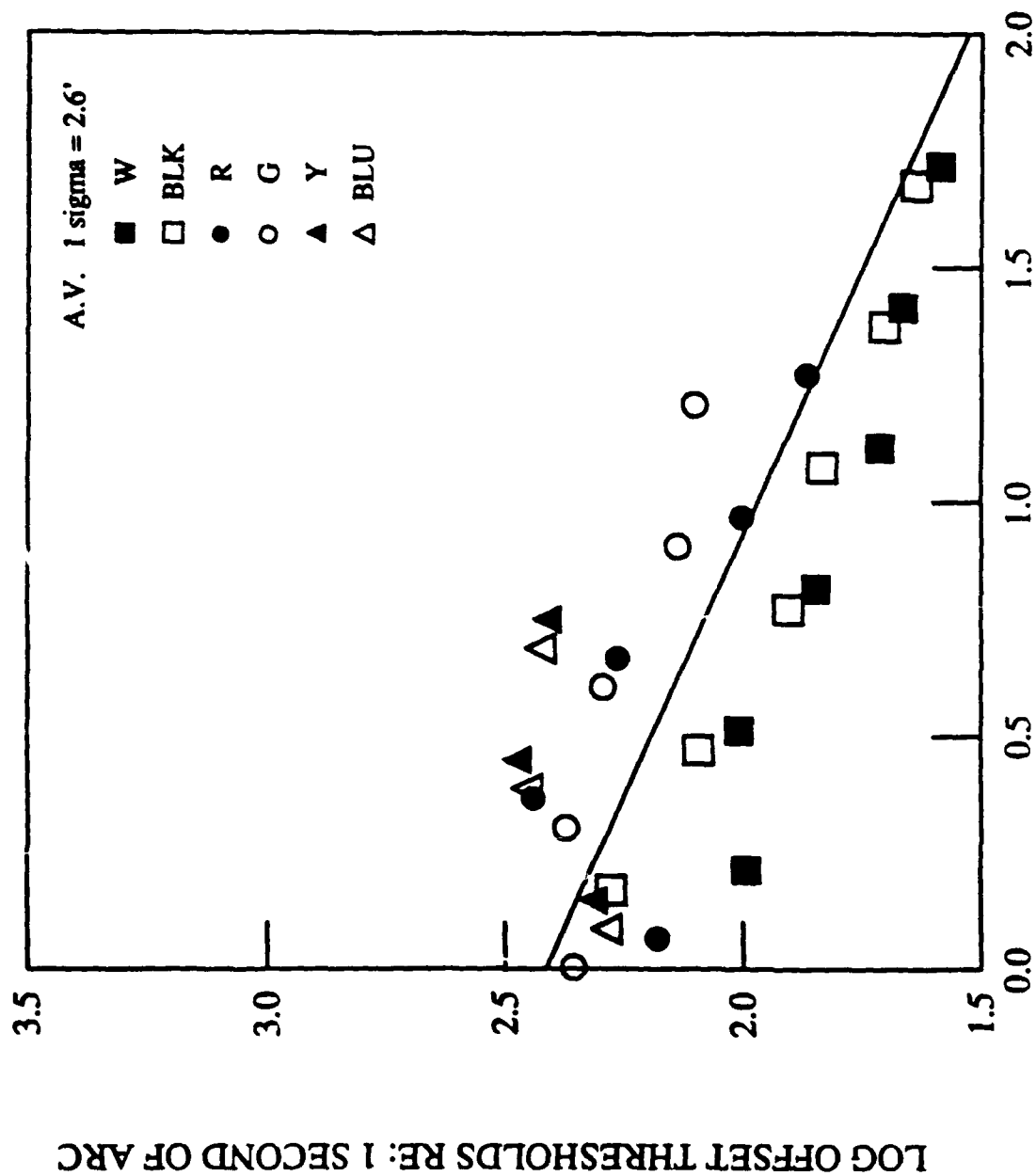
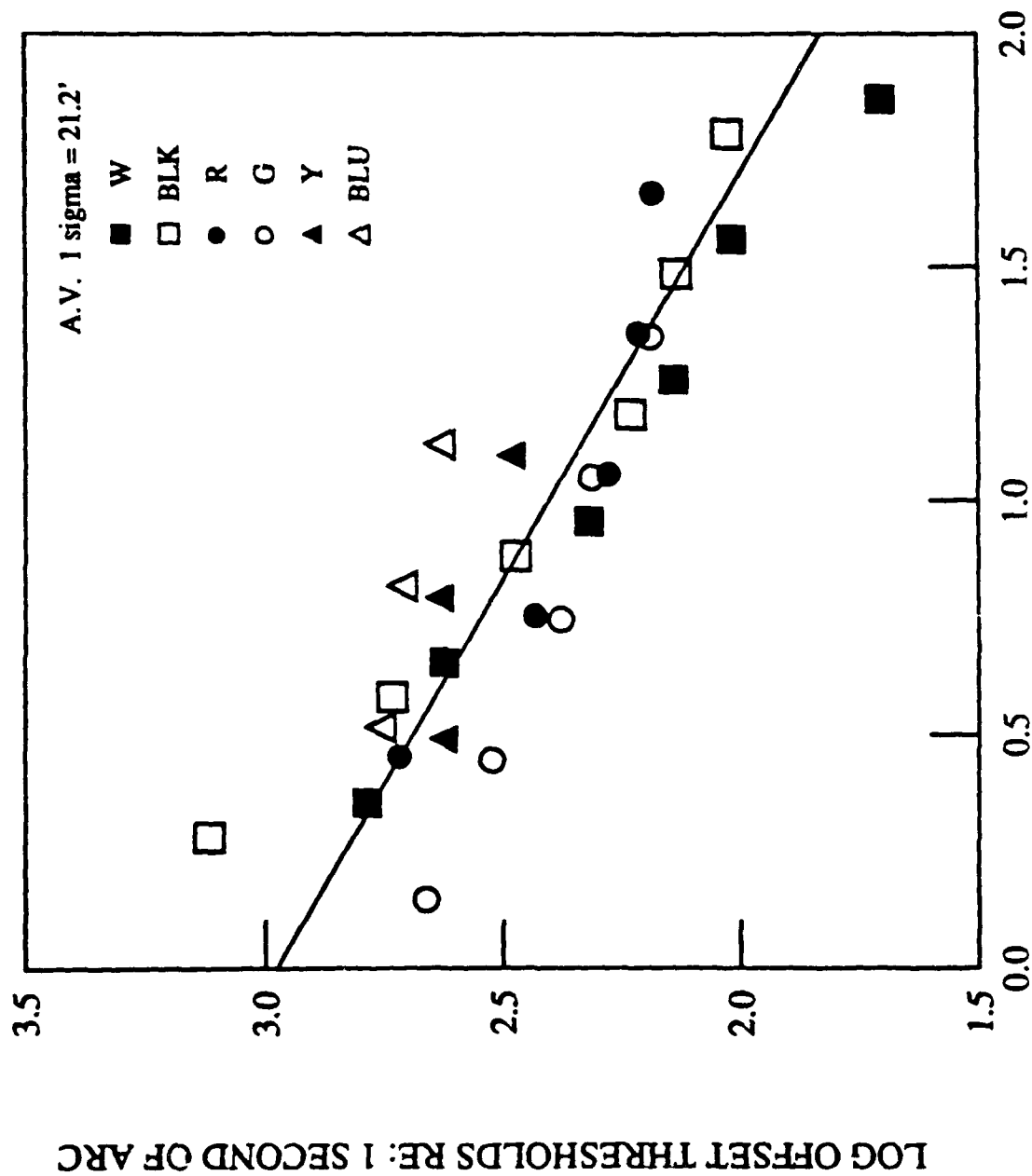


FIGURE 2

OFFSET THRESHOLDS



LOG CONTRAST RE: DETECTION THRESHOLDS

OFFSET THRESHOLDS

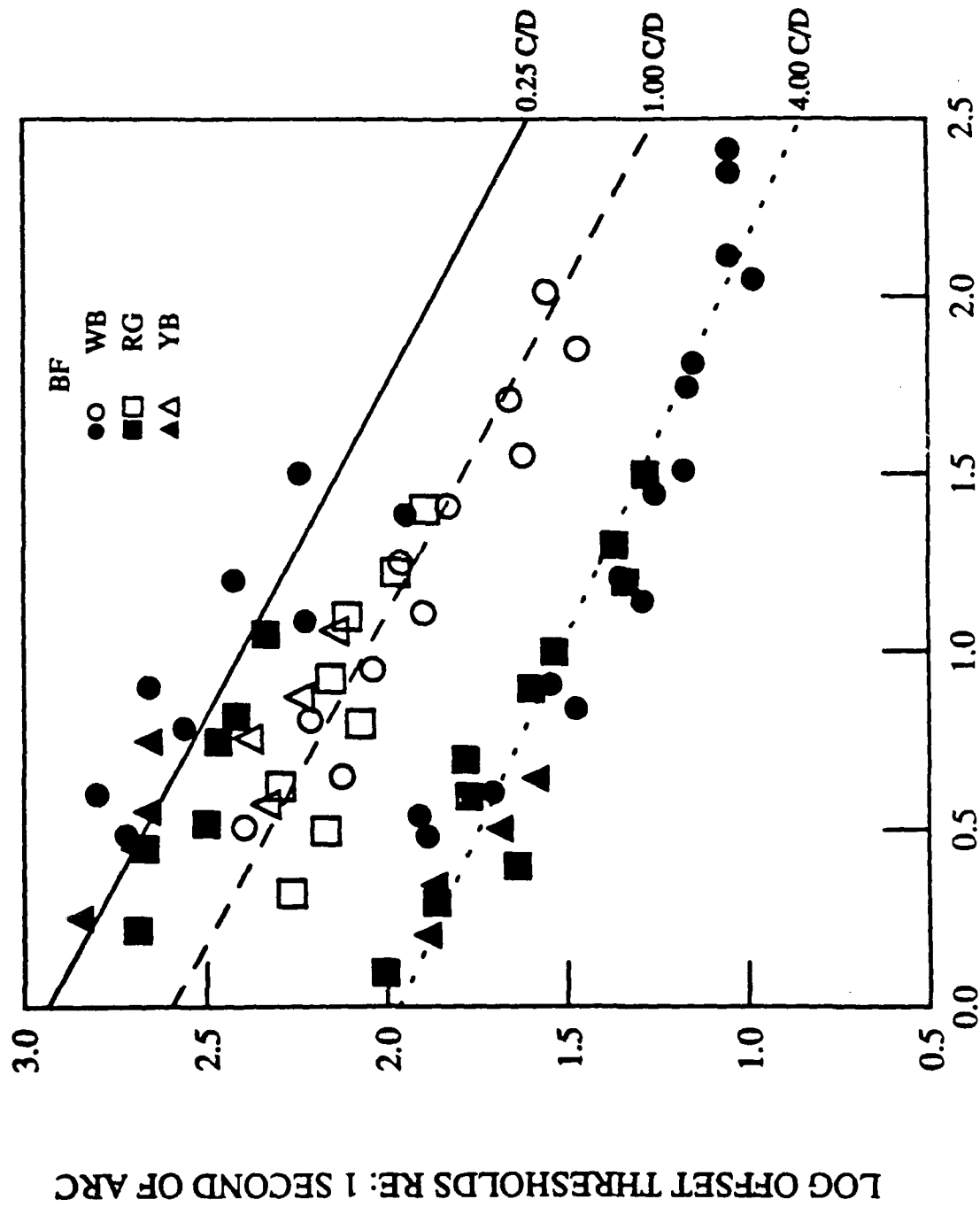


FIGURE 1 LOG CONTRAST RE: DETECTION THRESHOLDS

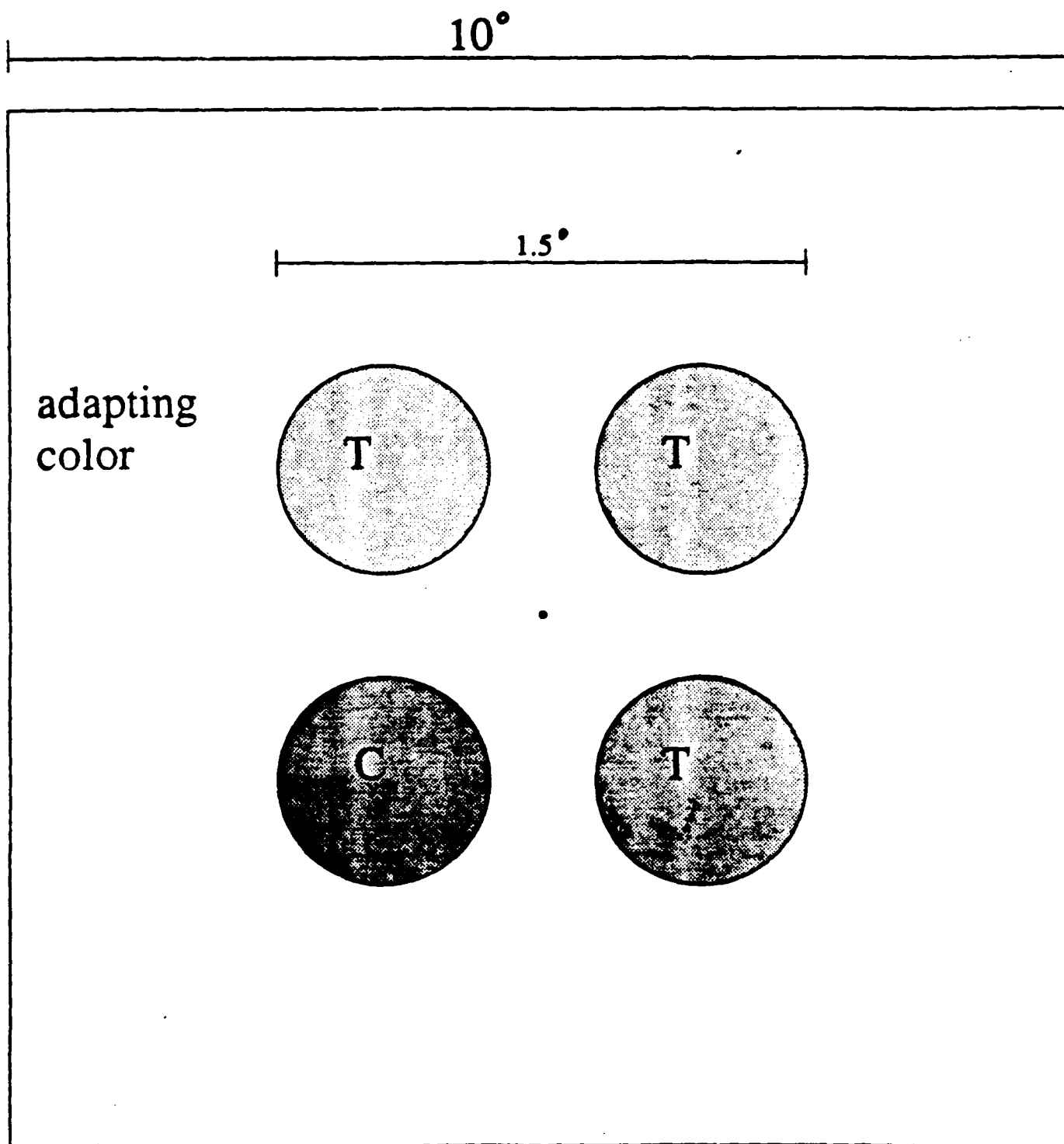


FIGURE 5

ISOLUMINANT PLANE

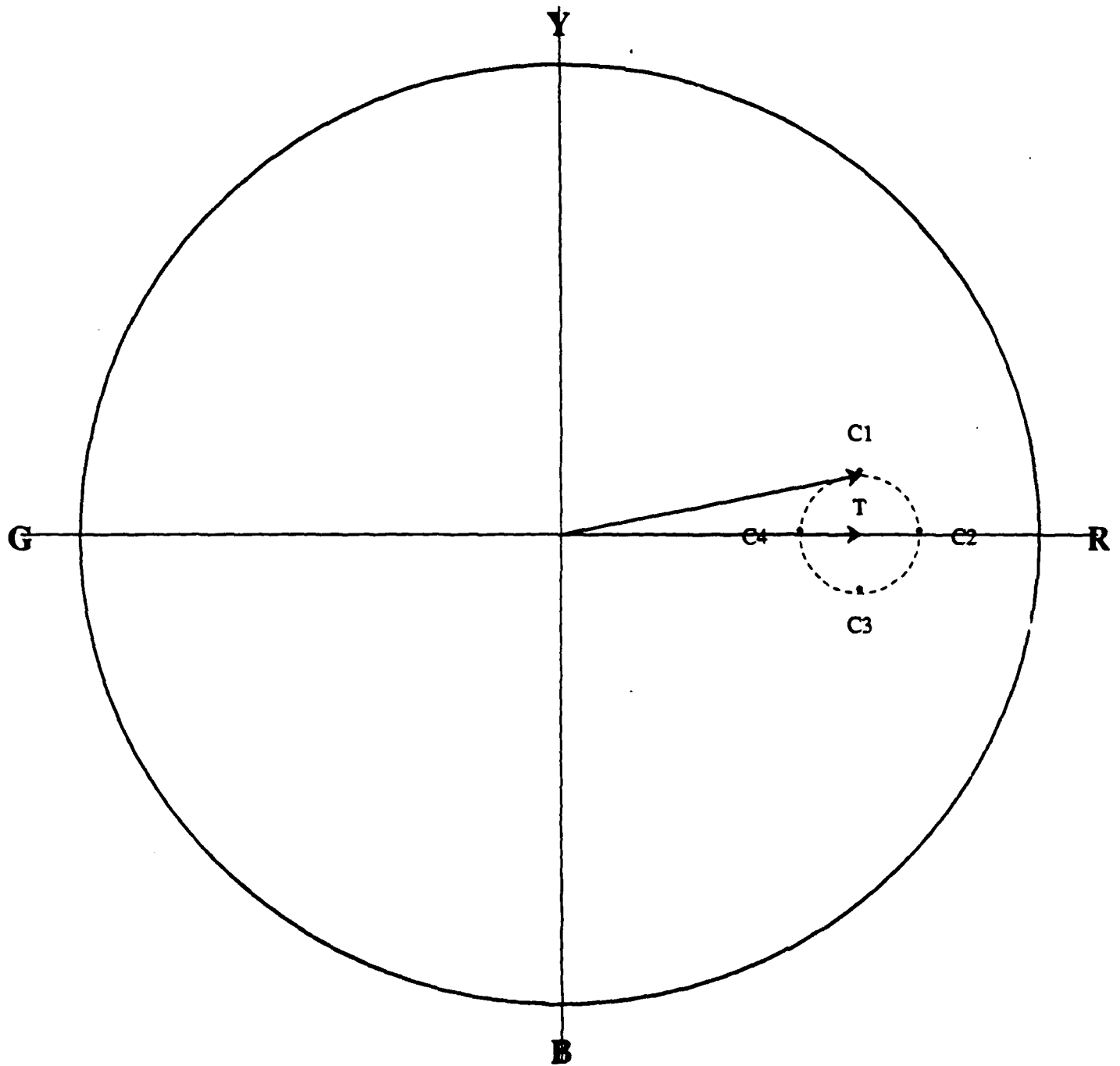


FIGURE 6

TEST AND COMPARISON ALONG SAME AXIS

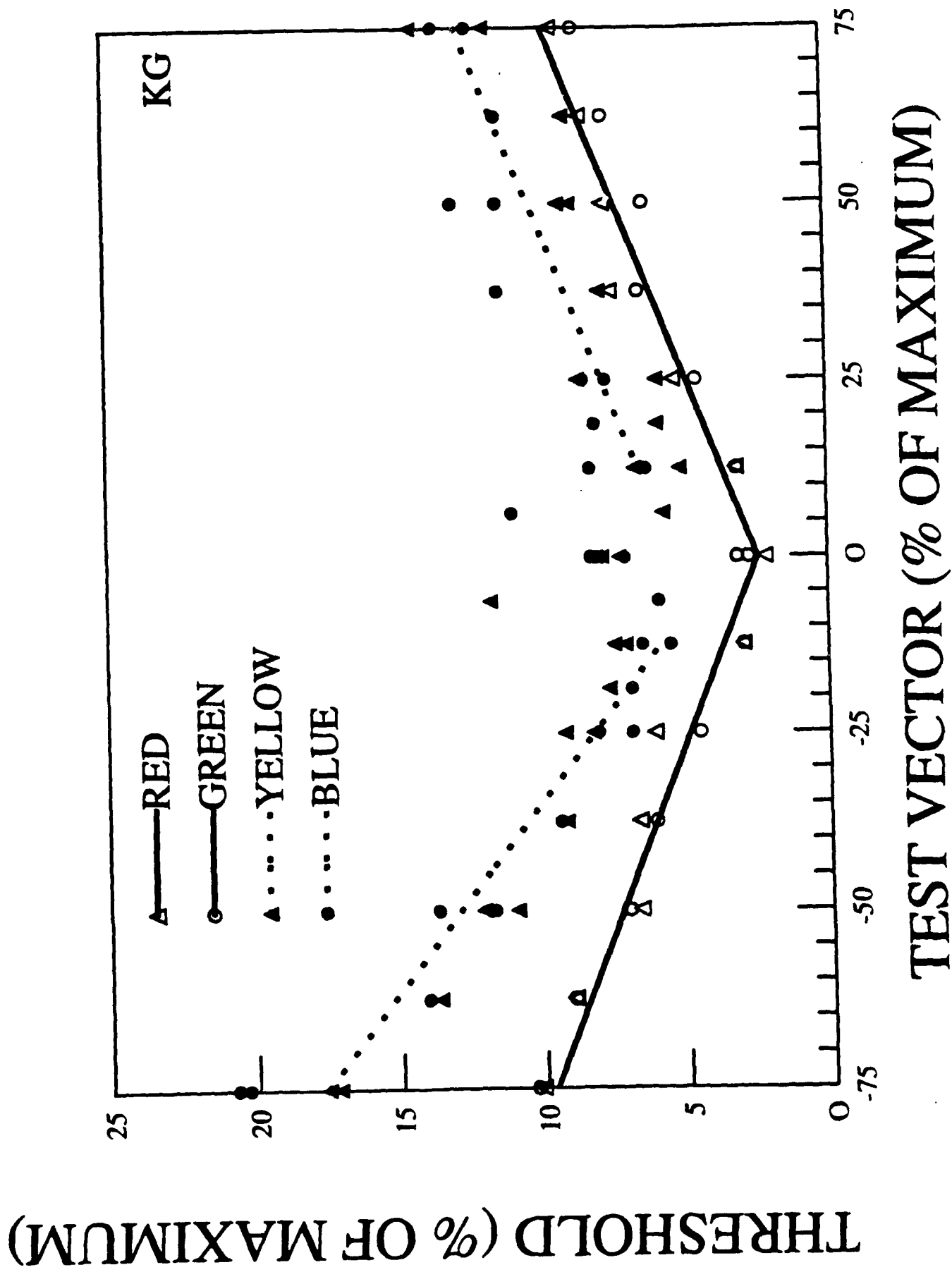
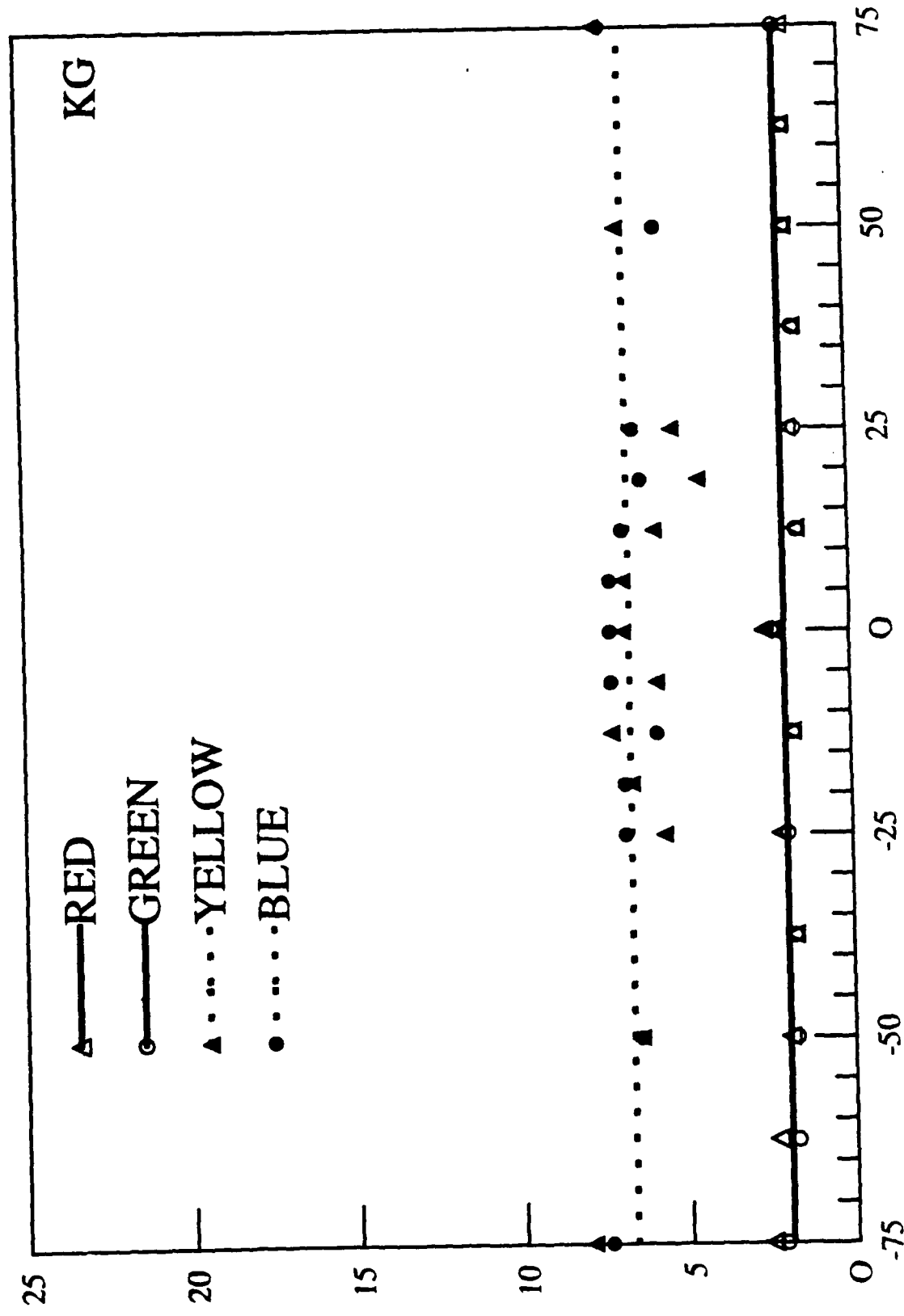


FIGURE 7

TEST AND COMPARISON ORTHOGONAL

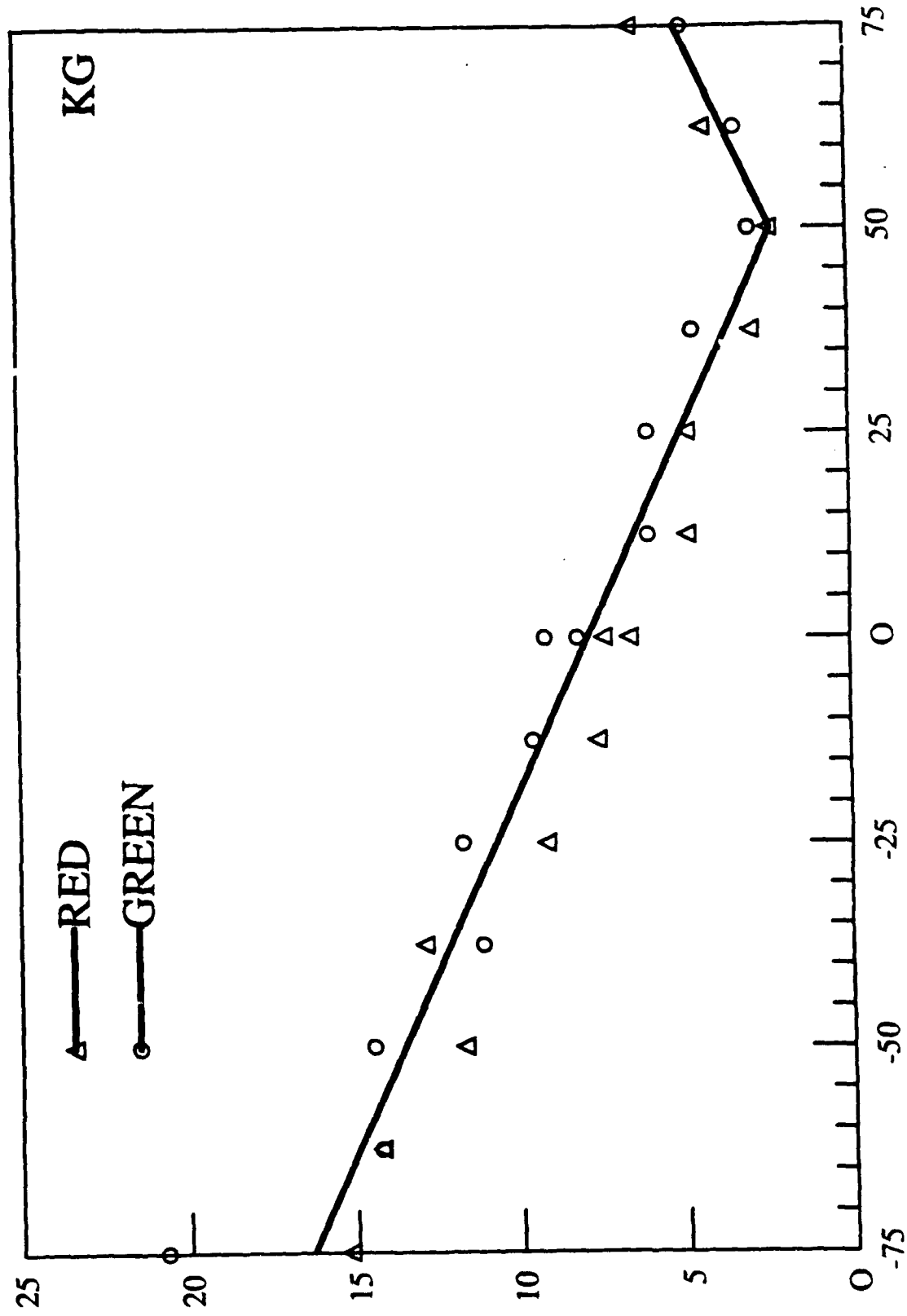
THRESHOLD (% OF MAXIMUM)



TEST VECTOR (% OF MAXIMUM)

ADAPTATION POINT RED

THRESHOLD (% OF MAXIMUM)



LOCATION OF TEST COLOR ON CONSTANT B AXIS